NSF-DEB-9815500- FINAL REPORT, COLLABORATIVE RESEARCH, "LATE HOLOCENE EXPANSION OF UTAH JUNIPER IN WYOMING: A MODELING SYSTEM FOR STUDYING ECOLOGY OF NATURAL INVASIONS",

Steve Jackson (University of Wyoming) and Julio Betancourt (University of Arizona).

This project used synoptic surveys of ^{14}C dated woodrat middens to document the migrational history of Utah juniper, ponderosa pine, and Colorado pinyon (Pinus edulis) in the central Rocky Mountains of northeastern Utah, Wyoming, southern Montana, and South Dakota. Both the Utah juniper and ponderosa pine studies included construction of biogeographic models. In addition, the project generated tree-ring reconstructions of precipitation over the past millennium in two of the key basins, the upper Colorado and Bighorn Basin. These reconstructions were used to examine the role of decadal to multidecadal precipitation variability in plant migration. Also, more than 80 historical photographs were located and matched to gage the expansion of Utah juniper over the last century. Thus far, the project has produced 10 articles in high-visibility journals and 3 Ph.D dissertations, training of several graduate and undergraduate students, multiple presentations at national and international meetings, and a workshop with local land managers in Wyoming.

I. Dynamics of Utah Juniper Migration: Role of Landscape Structure and Climate Variability

Ecologists are devoting considerable effort to understanding and modeling mechanisms underlying biological invasions. Prehistoric plant migrations can serve as model systems for understanding ongoing and future natural invasions, as well as for studying how landscape structure and climatic variability influence both alien and natural invasions over timescales of centuries to millennia.

Paleoecological studies of plant migration require spatial networks of time-series data that record local establishment and expansion of populations. In reconstructing plant migrations using pollen stratigraphies, some pitfalls include a lack of taxonomic precision (e.g., most pollen grains can only be identified to family or genus), and the inability to discriminate between small, local populations and distant, regional ones. Packrat midden analysis overcomes these pitfalls. Plant macrofossils in middens usually can be identified to species, and originate from plants growing within 50 meters of the packrat den.

Beginning in 1998, the Desert Laboratory teamed up with Steve Jackson and his Quaternary Plant Ecology Laboratory at the University of Wyoming to reconstruct migrational histories at the northern distributions of key woodland trees (Utah juniper, pinyon pine, and ponderosa pine) in the Central Rockies. The effort involves synoptic development of packrat midden chronologies along presumed pathways for Holocene migration.

Holocene migration of Utah juniper into central and northern Wyoming and southern Montana from the south proceeded by a series of long-distance dispersal events, which were paced by climate variability and structured by the geographic distribution and connectivity of suitable habitats on the landscape. Its migration into the region involved multiple long-distance dispersal events, ranging from 30 to 135 kilometers.

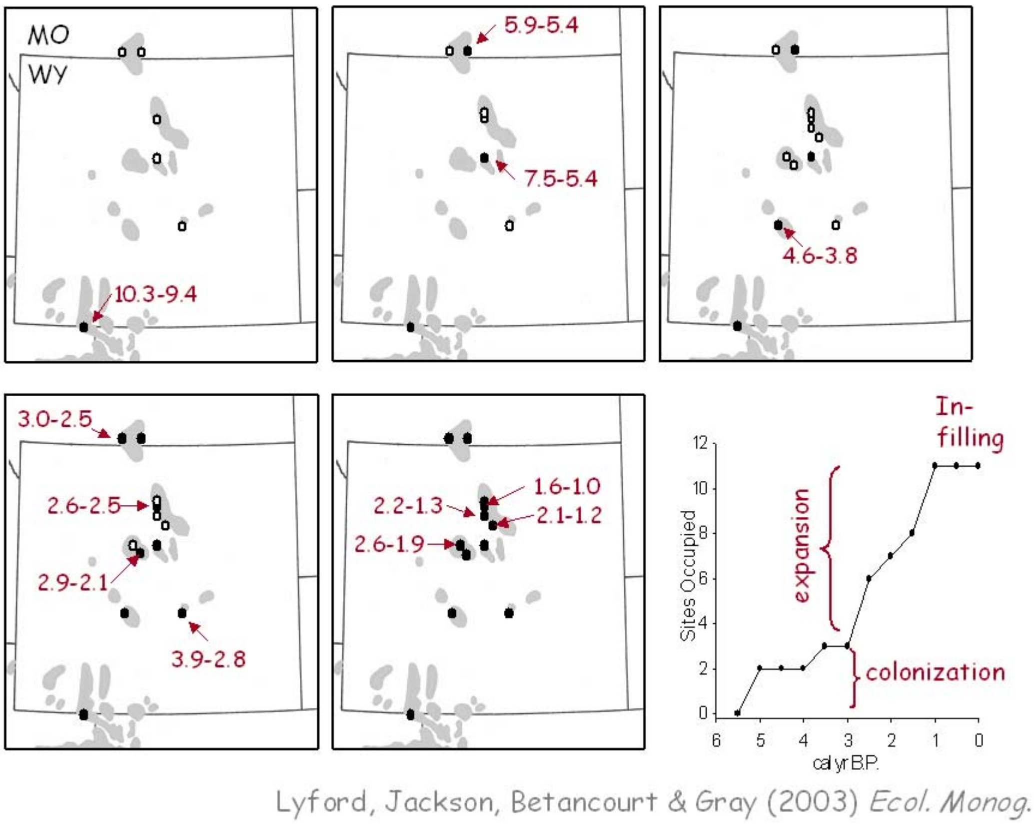

Figure 1. Map of Wyoming and adjoining state showing patchy distribution of Utah juniper (*Juniperus osteosperma*) in gray and bracketing dates (in thousands of calendar years before present) and sequence of arrival at each of 12 sites where midden series were developed. Open circles denote absence, closed ones presence of Utah juniper in midden series.

One of the earliest-established populations, on East Pryor Mountain in south-central Montana, is currently the northernmost population and among the most favorable sites for Utah juniper. Establishment by long-distance dispersal of that population and another in the Bighorn Basin occurred during a period of relatively dry climate between 7500 and 5400 years ago. Further expansion of these initial colonizing populations and backfilling to occupy suitable sites to the south was delayed during a wet period from 5400 to 2800 years ago. Development of dry conditions 2800 years ago led to a rapid expansion in which Utah juniper colonized sites throughout its current range. Recent encroachment of Wyoming grasslands by Utah juniper is probably due to the effects of livestock grazing, though increasing tree densities on rockier terrain may represent continued infilling of populations after late Holocene expansion.

Our migration studies indicate that landscape structure and climate variability play important roles in governing the pattern and pace of natural invasions, and deserve close attention in studying and modeling plant invasions, whether alien or natural. Finally, arrays of populations with different, known dates of colonization provide a natural experiment to evaluate the influence of time on the evolution of population, community and ecosystem properties hundreds to thousands of years after invasion

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Lyford, M.E., Jackson, S.T., Gray, S.T., Eddy, R.G. 2004. Validating the use of woodrat (*Neotoma*) middens for documenting natural invasions. *Journal of Biogeography* 31:333-342.

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Lyford, M.E. 2001. The roles of dispersal, climate, and topography in the Holocene migration of Utah juniper into Wyoming and southern Montana. Ph.D. Dissertation, University of Wyoming, Laramie, WY.

II. Climatic Distribution and Holocene Dynamics of Ponderosa Pine Migration in the Central Rockies

Ponderosa pine (*Pinus ponderosa*) is an economically and ecologically important conifer that has a wide geographic range in the western U.S.A., but is mostly absent from the geographic center of its distribution - the Great Basin and adjoining mountain ranges. Much of its modern range was achieved by migration of geographically distinct Sierra Nevada (*P. ponderosa* var. *ponderosa*) and Rocky Mountain (*P. ponderosa* var.

scopulorum) races in the last 10,000 years. Previous research has confirmed genetic differences between the two varieties, and measurable genetic exchange occurs where their ranges now overlap in western Montana. Different approaches in bioclimatic modeling are required to explore ecological differences between varieties and their implications for historical biogeography and impending changes in western landscapes.

We used a classification tree analysis and a minimum volume ellipsoid as models to explain the broad patterns of distribution of ponderosa pine in modern environments using climatic and edaphic variables. Most biogeographic modeling assumes that the target group represents a single, ecologically uniform taxonomic population. Classification tree analysis is resistant to this assumption because it allows the creation of pathways that predict multiple positive and negative outcomes. Thus, classification tree analysis can be used to test the ecological uniformity of the species. In addition, a multi-dimensional ellipse was constructed to describe the niche of each variety of ponderosa pine, and distances from the niche were calculated and mapped on a 4-km grid for each ecological variable.

The resulting classification tree identified three dominant pathways predicting ponderosa presence. Two of these three pathways correspond roughly to the distribution of var. *ponderosa*, and the third pathway generally corresponds to the distribution of var. *scopulorum*. The classification tree and minimum volume ellipsoid model show that both varieties have very similar temperature limitations, although var. ponderosa is more limited by continental temperature extremes. The precipitation limitations of the two varieties are seasonally different, with var. ponderosa requiring significant winter moisture and var. *scopulorum* requiring significant summer moisture.

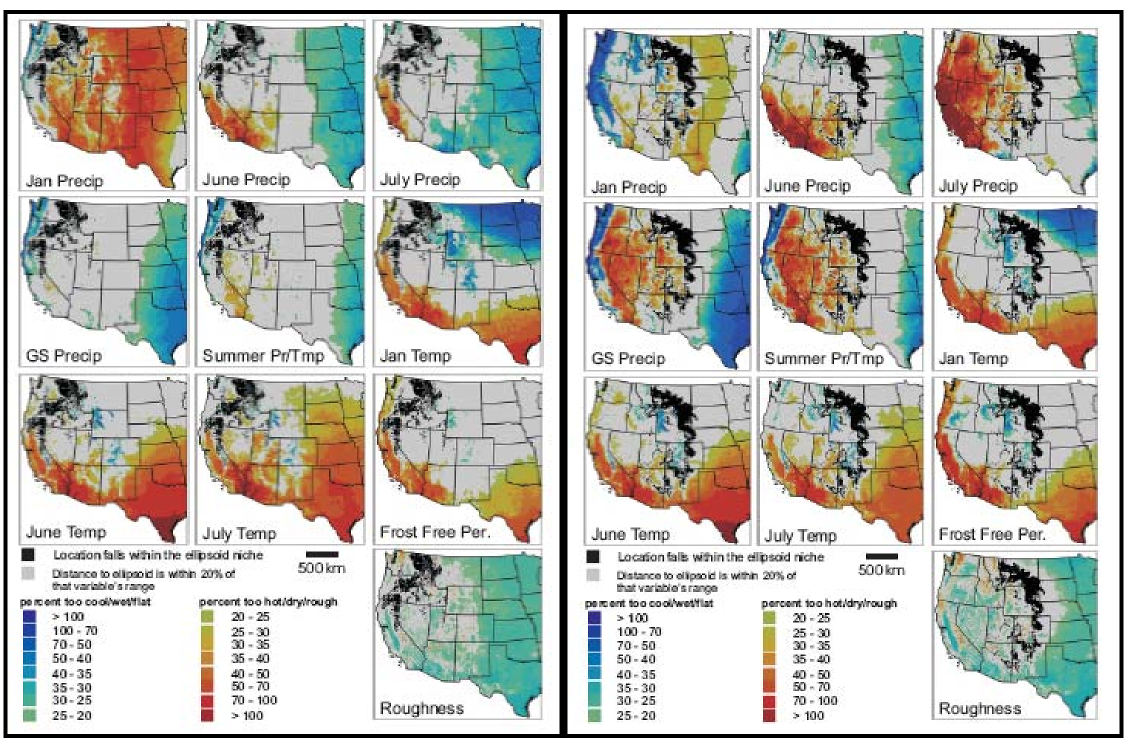

Figure 2. Calculated distances to the ellipsoid niche of var. *scopulorum* (a) and var. *ponderosa* (b) expressed as a percentage of the total range for 10 climatic variablesThe varieties have very similar maps for temperature variables, but show seasonal differences for precipitation variables.

The classification tree analysis indicates that var. ponderosa is ecologically as well as genetically distinct from var. *scopulorum*. Ecological differences may maintain genetic separation in spite of a limited zone of introgression between the two varieties in western Montana. Two hypotheses about past and future movements of ponderosa pine emerge from our analyses. The first hypothesis is that, during the last glacial period, colder and/or drier summers truncated most of var. *scopulorum*'s range in the central Rockies, but had less dramatic effects on the more maritime and winter-wet distribution of var. *ponderosa*. The second hypothesis is that, all other factors held constant, increasing summer temperatures in the future should produce changes in the distribution of var. scopulorum that are likely to involve range expansions in the Central Rockies with warming of mountain ranges currently too cold but sufficiently wet in summer for var. *scopulorum*. Finally, our results underscore the growing need to focus more on genotypes than species in biogeographic modeling and ecological forecasting.

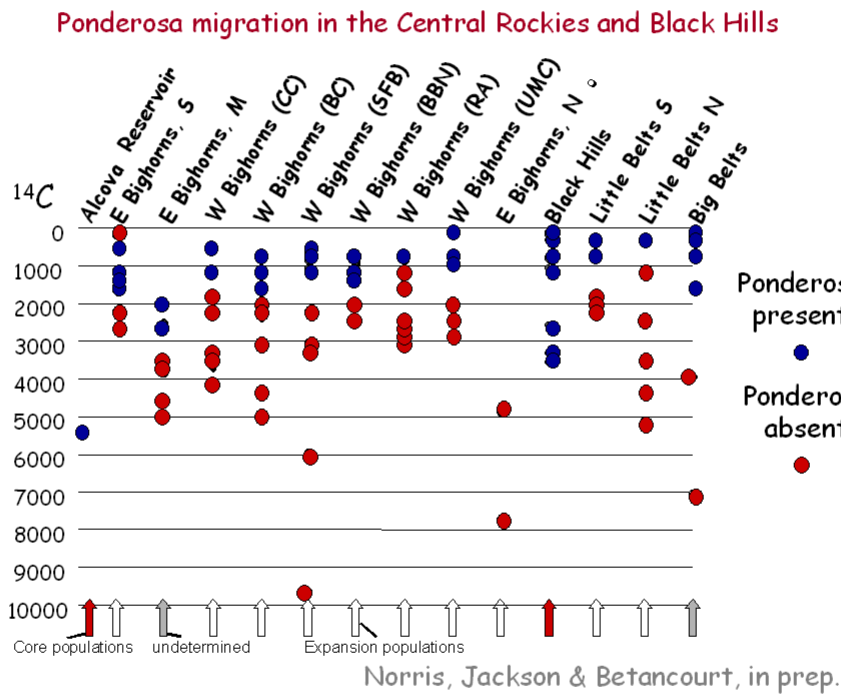

Figure 3. Presence/absence of ponderosa pine in woodrat middens from the central Rockies and Black Hills showing late Holocene (<4000 yrs ago), except in southern Wyoming and the Black Hills.

In addition to bioclimatic modeling, we conducted a synoptic survey and analysis of woodrat middens from the central Rockies (Wyoming, Montana, and South Dakota) to determine the Holocene migrational history of var. *scopulorum*. We found this migrational history to parallel that of Utah juniper, with initial colonization in southern Wyoming and South Dakota sometime prior to 6000 yr B.P. and rapid expansion in the period from 2600 to 1000 yr B.P. This duplication of migrational timing for two key, woodland species strongly suggests a climatic driver, primarily warming and drying that must have occurred with increased, global solar irradianc at that time. A dissertation on ponderosa pine migrational dynamics and climatic distribution should be completed by Jody Norris in 2005.

Norris, J., Jackson, S. T., and Betancourt, J.L. 2005. A classification tree analysis of the distribution of ponderosa pine in the western U.S. *Journal of Biogeography* (in press).

Norris, J. 2005. Bioclimatic distribution of ponderosa pine and Holocene migrational dynamics in the central Rocky Mountains. Ph.D. dissertation in progress, University of Wyoming.

III. Role of multidecadal climate variability in Pinyon (*Pinus edulis*) pine migration in the Central Rockies

Evidence from woodrat middens and tree rings at Dutch John Mountain (DJM) in northeastern Utah reveal spatiotemporal patterns of pinyon pine (*Pinus edulis*) colonization and expansion in the past millennium. Our woodrat midden studies determined that the DJM population, an isolated northern outpost of pinyon, was established by long-distance dispersal from more contiguous populations 40 km south. Expansion of this isolate was markedly episodic, and tracks multidecadal variability in precipitation reconstructed from our own tree ring studies in the area. Initial colonization occurred ~AD 1246 but expansion was forestalled by catastrophic drought from AD 1250-1288, which we speculate produced massive dieoffs of Utah Juniper, the dominant tree at DJM for the previous ~8700 years. In the wake of these possible dieoffs and a few wet decades (AD 1330-1339 and 1368-1377), pinyon quickly replaced Utah juniper across DJM. Further spread was again delayed by droughts in AD 1398-1410 and 1491-1512. Through continued expansion episodes in recent centuries pinyon became the dominant species at DJM until a ~10,000-ha fire in summer 2002. This fire destroyed almost all of the pinyon stands at DJM and reset demographic clocks that may facilitate other novel invasions. The fire compromised the potential of the site for ecological and genetic studies in the context of a well-documented founder event, and indicates a growing need for "salvage paleoecology" to counter accelerated loss of critical information in the face of increased disturbance.

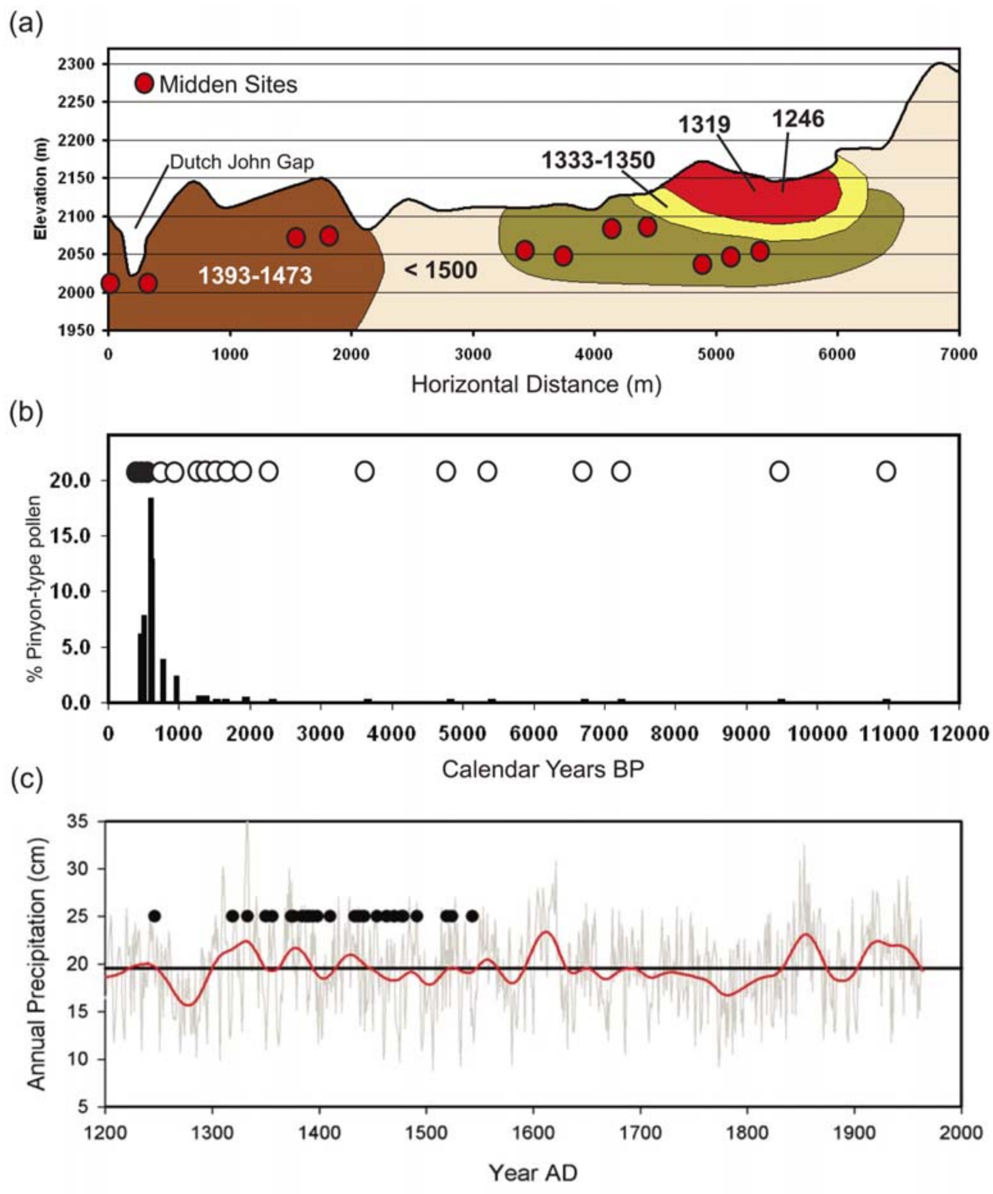

Figure 4. (a) Percentages of pinyon-type pollen (black vertical bars) and presence (black dots) or absence (open circles) of pinyon pine macrofossils from 12,000 yrs of midden record collected at Dutch John Mountain. (b) Profile map of the Dutch John Mountain study area showing dates for the invasion and expansion of pinyon pine as reconstructed from tree-ring data. (c) Ages for the 33 oldest trees in the study area (black dots) plotted against reconstructed annual (grey lines) and 30 yr smoothed (red line) precipitation values for the Uinta Basin Region.

Long-term ecological dynamics have traditionally been viewed as steady-state processes occurring against a backdrop of randomly fluctuating or gradually changing conditions. Variations in climate, however, are rarely random or gradual. High-resolution records from tree-rings and other sources indicate that climate of the past few millennia was characterized by episodic behavior, with variability occurring across a range of temporal scales, and punctuated by frequent regime shifts, defined as abrupt changes from one mode of variability to another.

Precipitation variability over decadal to multidecadal timescales and the accompanying regime-like behavior is a particularly strong and consistent feature of western North America's climate. Evidence from our pinyon, Utah juniper and ponderosa pine migration studies indicate that the late-Holocene migrations of many woodland species were paced by episodic precipitation variability, with alternating periods of rapid expansion and stasis. Decadal to multidecadal climate variability may modulate the frequency of dispersal events and the distance they cover. In addition, switching between precipitation regimes alternately increases or decreases the probability of survival and reproduction after arrival in a new habitat. Shifting climate regimes influence the density of favorable habitats for a species across the landscape, as well as altering competitive interactions and disturbance processes.

Most theoretical and analytical models of plant migration and vegetation dynamics fail to incorporate episodic climate variability. Such models usually treat climate as a static mean, a white-noise process, or linear trend. Not only does this limit our understanding of past plant migrations and the development of modern landscapes, this oversight may greatly hinder efforts to forecast future vegetation transitions. Forecast models for plant migration and vegetation change also seldom address the geographic dimensions of episodic climate variability. In the case of precipitation, growing evidence suggests that most prolonged dry-regimes affect large areas of western North America synchronously. Furthermore, the pluvial regimes that often follow such "megadroughts" are equally widespread.

The effects of climatic regime shifts over regional to sub-continental scales may be especially hard to forecast given the high potential for cross-scale interactions. In the case of vegetation change driven by drought-induced disturbance and mortality, processes taking place at the regional level may also influence landscape dynamics, thus inducing feedbacks between finer and coarser scales. In the initial phases of a migration event, the combination of episodic invasions linked to climatic regimes and long-distance dispersals tends to produce a patchy distribution for the new species at landscape to regional scales. As the migration progresses, population and dispersal processes in each of these patches can lead to episodic backfilling of unoccupied habitats or the extinction of some satellite populations. Years, decades, or centuries of failed or limited invasions may alternate with periods of rapid establishment and expansion.

The Dutch John population is one of two peripheral isolates of *Pinus edulis* -the other being Owl Canyon in northeastern Colorado - known to have originated from long-distance dispersal events within the past millennium. Such founder populations offer model systems for evaluating genetic consequences, intrinsic rates of population growth, local pathways and rates of expansion, and community and ecosystem-level responses associated with natural tree invasions.

IV. Precipitation Variability in the central Rockies

Recent and ongoing droughts emphasize the importance of understanding precipitation variability on not just water resources, but also on climate's influence on plant migration and vegetation change. We used ancient tree rings to examine the timing and duration of severe dry spells and extended wet periods in two such areas, the Bighorn and Uinta Basins, critical to our plant migration studies. The Bighorn Basin represents 30% of the Yellowstone River's contribution to Upper Missouri River flows, while the Uinta Basin contributes about 10% of the inflow of the Colorado River into Lake Powell. Both the Bighorn and Uinta Basins are managed on the basis of gaged streamflow since 1900. Questions remain about whether or not the instrumental record adequately represents the long-term risk to water resources from sustained drought.

Published in *Journal of Climate*, a tree-ring reconstruction of precipitation from A.D. 1260 to 1998 for the Bighorn Basin of northern Wyoming/southern Montana shows that regional hydroclimatic variability was dampened in the instrumental era (post-1900) compared to the previous 640 years. Both single-year and decadal-scale droughts were more severe before 1900, and multi-year droughts tended to last much longer. This reconstruction also shows that regional droughts of magnitude and duration similar to the current (1999-2004) drought have been common occurrences for at least the last seven centuries.

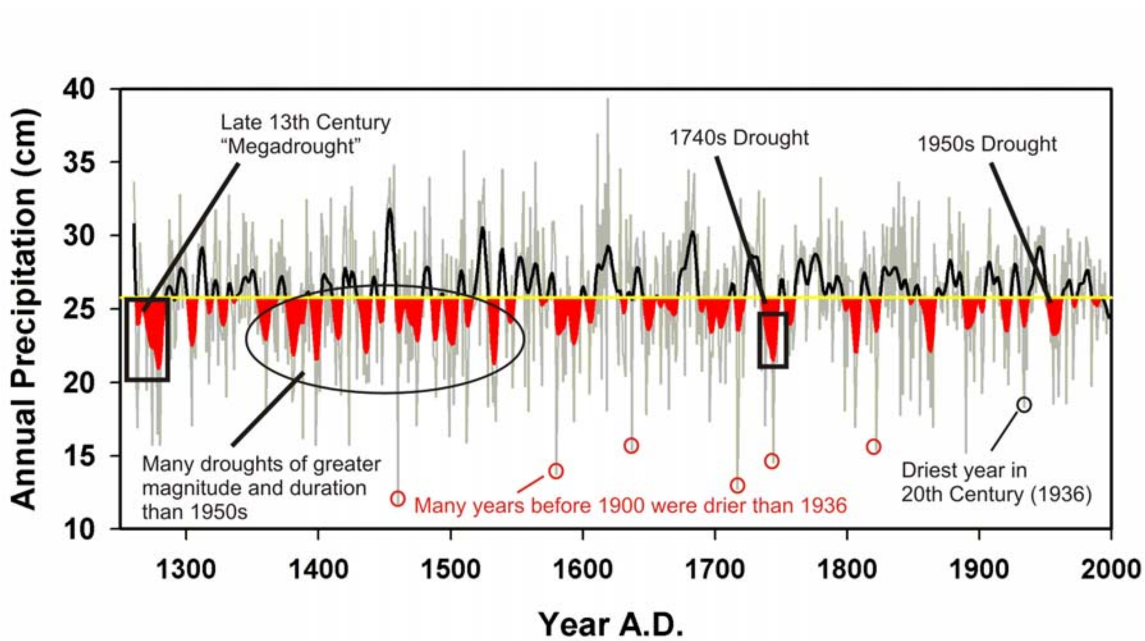

Figure 5. Plot of reconstructed annual precipitation for the Bighorn Basin region of northern Wyoming and southern Montana (1260-1998 AD). The graphs also shows a 10-yr running average of precipitation values with drought periods highlighted in red.

Results from a similar study in the Uinta Basin of northeastern Utah (September issue *Journal of the American Water Resources Association*) demonstrate that single-year dry events in this region also tended to be more severe than those after 1900, and multi-year droughts were longer and more severe prior to 1900. In particular, dry events in the late 13th, 16th and 18th Centuries surpass the magnitude and duration of droughts seen in the

Uinta Basin after 1900. The last four decades of the 20th Century represent one of the wettest periods since A.D. 1226.

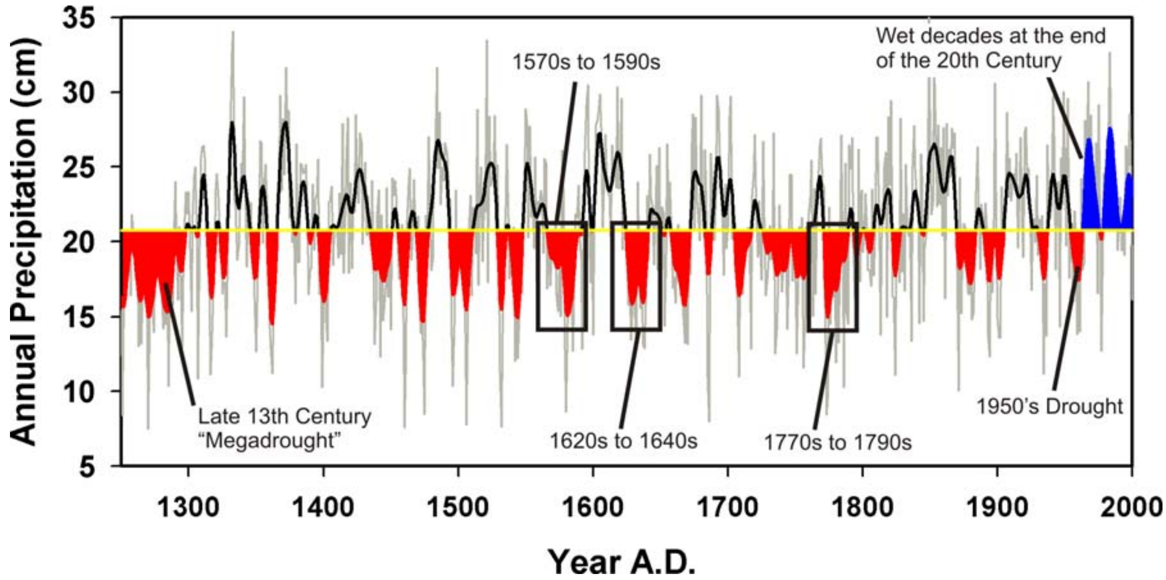

Figure 6. Reconstructed precipitation for the Uinta Basin of northeastern Utah (1226-2001 AD). Drought periods are shown in red. Wet decades in the late 20th Century are shown in blue.

Given the overall wetness and lack of extreme droughts in the twentieth century, water-planning based on the instrumental record clearly underestimates the risk of drought in both the Bighorn and Uinta Basins. These studies show instead that mitigation and planning efforts must consider a wider range of climatic scenarios, including droughts of different lengths, magnitudes, and intensities than those presented by the instrumental record. Managers should also consider numerous combinations of wet/dry events in their decision-making. Furthermore, planning efforts could focus more on the potential for long-duration dry events rather than average values for water availability.

Gray, S. T. 2003. Long-term climate variability and its implications for implications for ecosystems and natural resource management in the central Rocky Mountains. Ph.D. dissertation. University of Wyoming, Laramie, WY, 130 pp.

Gray, S. T., Betancourt, J. L., Fastie, C. L., Jackson, S. T. 2003. Patterns and sources of multidecadal oscillations in drought-sensitive tree-ring records from the central and southern Rocky Mountains. *Geophysical Research Letters*, v. 30, no. 6, p. 49-1 - 49-4, doi:10.1029/2002GL016154.

Gray, S. T., Fastie, C., Jackson, S. T., and Betancourt, J. L. 2004. Tree-ring based reconstruction of precipitation in the Bighorn Basin, Wyoming since A.D. 1260. *Journal of Climate* 17, 3855-3856.

Gray, S. T., Jackson, S. T., and Betancourt, J. L. 2004. Tree-ring based reconstructions of interannual to decadal-scale precipitation variability for northeastern Utah since 1226 A.D. *Journal of the American Water Resources Association* v. 40, p. 947-960.

V. Repeat Historical Photography of Twentieth Century Vegetation Change in Wyoming and Montana

Historical photographs of landscapes ranging from hillslopes and mountain peaks to wetlands are available for nearly any area in the western United States. As a first approximation, environmental changes of the past century can be assessed by finding the site of an historical photograph, relocating the original camera position, and making a new photograph of the same scene at the same scale and dimension. Differences between historical and repeat photographs provide a basis for identifying and even quantifying changes, while the new photograph establishes a benchmark for future evaluation. Ground repeat photography is a simple, inexpensive, and elegant tool for reconstructing past environmental changes and monitoring future changes, and is particularly well-suited for the open landscapes of the western U.S.

Historical photographs (ca. 1860-1930) are readily available in a variety of archives. For example, one of the requirements in the early days of the U.S. Geological Survey was for its geologists to photograph outcrops they were describing and mapping. Consequently, a rich archive of both high quality negatives and positives of western landscapes, many taken with large format cameras, has accumulated at the USGS Photo Library in Denver, Colorado.

As part of the overall project, Steve Tharnstrom and Julio Betancourt matched historical photographs throughout Wyoming, taken in the early part of this century. This repeat photography effort is intended to document changes in the distribution of Utah juniper (Juniperus osteosperma) and other key plant species during the past 100 years.

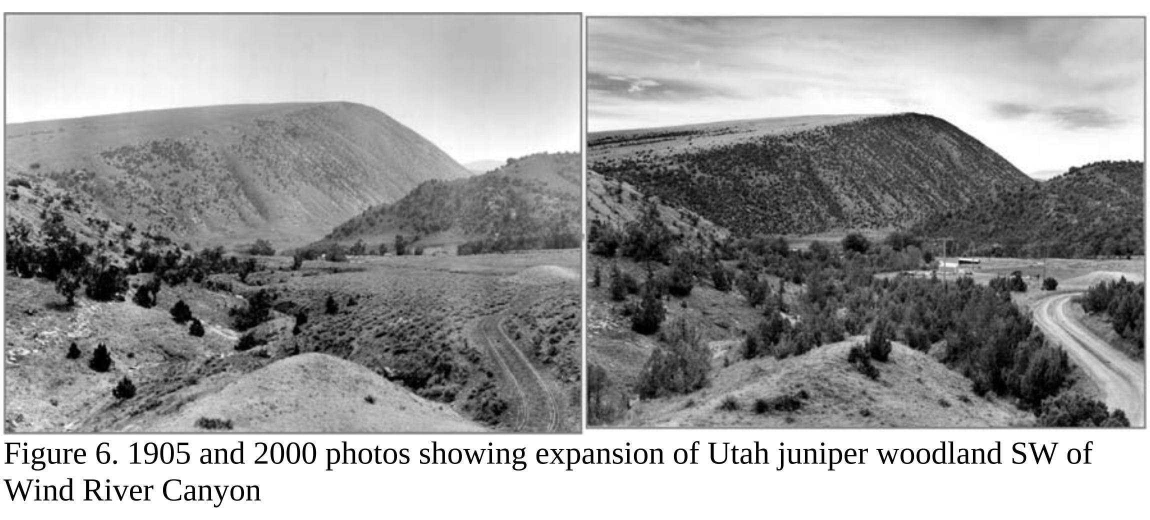

Figure 6. 1905 and 2000 photos showing expansion of Utah juniper woodland SW of Wind River Canyon